

Zusammenfassung

Jahreszeitliche Änderungen in der Futterzusammensetzung der indischen Falschen Vampirfledermaus, Megaderma lyra lyra, in Rajasthan

Untersuchungen über die jahreszeitliche Zusammensetzung der Nahrung der indischen Falschen Vampirfledermaus, *Megaderma lyra lyra*, wurden in verschiedenen Gebieten Rajasthans durchgeführt. Diese Art frisst Insekten zu allen Jahreszeiten, lebt im Winter aber nur von Käfern. Zusätzlich werden verschiedene Vertebraten (Reptilien, Amphibien, Fische und sogar Vögel) erbeutet. Im Winter, und wenn im Sommer Insekten nicht in ausreichender Menge vorhanden sind, besteht die Nahrung vorzugsweise aus Wirbeltieren.

M. lyra lyra frisst eine Reihe von pflanzenpathogenen Insekten. Ihr kommt somit eine bedeutende Rolle in der biologischen Schädlingsbekämpfung zu.

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A survey of gross stomach morphology in Microtinae (Rodentia: Muroidea)

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Abstract

Surveyed the gross stomach morphology of 55 species from 16 genera of Microtinae (Rodentia, Muroidea). Most species represent North American forms in order to complement VORONTSOV'S coverage of Old World species. Some of the interesting variations in gastric structure include: the separation of *Dicrostonyx* from *Synaptomys*, *Myopus* and *Lemmus*; the contrast between New and Old World *Lagurus*; the similarity of the North American Water Vole to other *Microtus* and its dissimilarity to Old World *Arvicola*; the extensive diversity encountered among specimens of *Clethrionomys gapperi*. In general, data from gastric anatomy is more in accord with a multitribal classification of the Microtinae rather than a dual tribal arrangement. The functional implications of the differences in gastric anatomy are discussed.

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Introduction

VORONTSOV's studies (1957, 1962, 1967) of the alimentary canal of myomorph rodents have revealed striking interspecific variation, involving not simply their dentitions but all segments of the digestive tract. Enlarging upon the earlier efforts of TOEPFER (1891) and TULLBERG (1899), VORONTSOV's comprehensive surveys have refocused attention on both the systematic utility of such differences as well as their functional importance. Within the Muridae (Myomorpha: Muroidea), major variations of the stomach occur that are discernable at the gross anatomical level (CARLETON 1973; VORONTSOV 1967). In this report, I have examined gastric morphology within one subfamily of Cricetidae, the Microtinae, with an intent to include many New World forms in order to complement VORONTSOV's coverage of Old World species.

Material and methods

The present study surveys 55 species representing 16 genera of microtine rodents, which are listed below together with the number of specimens examined and their general locality. Most specimens studied are contained in the University of Michigan Museum of Zoology; some are located in the American Museum of Natural History (AMNH), the National Museum of Natural History (USNM), and the University of Puget Sound Museum of Natural History (UPS).

Alticola roylei: India, Kashmir, 1 (USNM); USSR, Pamirs, 3.

Arvicola sapidus: Spain, Valencia, 1 (USNM).

A. terrestris: Belgium, Leige, 1 (USNM); Finland, Uudenmaan, 5.

Clethrionomys gapperi: Canada, Alberta, 1 (USNM); Labrador, 2 (USNM); Mackenzie, 3 (USNM); Ontario, 3; Quebec, 2; Colorado, Rocky Mtn. Nat. Park, 10; Idaho, Bonner Co., 4; Maine, Oxford Co., 2; Michigan, Alger Co., 2; Gogebic Co., 2; Marquette Co., 2; Otsego Co., 4; Montana, Park Co., 14; New York, Thompsons Co., 3; Oregon, Wallawa Co., 7; South Dakota, Pennington Co., 3; Tennessee, Cocke Co., 3 (USNM); Washington, Columbia Co., 1; Wyoming, Johnson Co., 2.

C. glareolus: Czechoslovakia, South Moravia, 1 (AMNH); England, Uttoxeter, 3 (AMNH); Finland, Uudenmaan, 7; Hungary, Batorliget, 2; West Germany, Niedersachsen, 4 (AMNH).

C. occidentalis: Oregon, Coos Co., 1 (UPS).

C. rufocanus: Korea, near Pammol, 3 (USNM).

C. rutilus: Alaska, Anchorage, 6; Nulato River, 1; Tonzona, 3 (USNM).

Dicrostonyx groenlandicus: Canada, Manitoba, 2.

D. hudsonius: Canada, Labrador, 1 (USNM).

Ellobius alaicus: USSR., Kirgiz SSR., 2.

E. fuscocapillus: Iran, Chesme Sangi, 2.

E. lutescens: USSR., Armenian SSR., 1.

E. talpinus: USSR, Kazakh SSR., 1; Tien Shan, 1.

Eothenomys melanogaster: Burma, Chimeli Pass, 3 (AMNH); Taiwan, Chuei-feng, 5 (USNM).

Hyperacrius fertilis: India, Kashmir, 1 (USNM).

Lagurus curtatus: Washington, Douglas Co., 3.

Lemmus lemmus: Norway, 3; USSR., Alexandrovskaya, 1.

L. obensis: USSR, Siberia, Plaver Bay, 1 (USNM).

L. sibiricus: Alaska, Point Barrow, 4.

Microtus afghanus: USSR., Turkmen SSR., 1.

M. arvalis: West Germany, Niedersachsen, 3.

M. californicus: California, San Mateo Co., 7.

M. chrotorrhinus: Canada, Quebec, 2 (USNM).

M. fortis: USSR, Primorskiy Krai, 1.

M. fulviventer: Mexico, Oaxaca, 5.

M. gregalis: USSR, Chitinskaya, 2.

M. guatemalensis: Mexico, Chiapas, 2.

M. longicaudus: Montana, Carbon Co., 3.

M. mexicanus: Mexico, Jalisco, 10.

M. miurus: Alaska, Kivilina, 3.

- M. montanus*: Wyoming, Johnson Co., 6.
M. nivalis: Iran, Teheran, 1 (USNM).
M. ochrogaster: Montana, Carbon Co., 3.
M. oconomus: Hungary, Pest, 1.
M. oregoni: Oregon, Tillamook Co., 5.
M. pennsylvanicus: Michigan, Washtenaw Co., 5.
M. pinetorum: North Carolina, Wiles Co., 5.
M. quasiater: Mexico, Hidalgo, 4.
M. richardsoni: Montana, Park Co., 3.
M. savii: Italy, Tuscany, 1 (USNM).
M. sikimensis: Nepal, Kashua Khola, 2.
M. socialis: Iran, Chesme Sangi, 2.
M. subterraneus: Hungary, Komarom, 1.
M. townsendii: Washington, Mason Co., 2.
M. xanthognathus: Alaska, Yukon Highway, 5.
Myopus schisticolor: USSR., North Ural Mts., 1.
Neofiber alleni: Florida, Alachua Co., 3.
Ondatra zibethicus: Michigan, Washtenaw Co., 2.
Phenacomys alpinus: Oregon, Coos Co., 3 (UPS); Lane Co., 1 (UPS).
P. intermedius: Canada, Quebec, 1 (USNM); Colorado, Rocky Mtn. Nat. Park, 2; Montana, Park Co., 1.
P. longicaudus: California, Humboldt Co., 2 (UPS); Mendocino Co., 1 (UPS); Sonoma Co., 2 (UPS); Oregon, Benton Co., 1 (UPS); Curry Co., 2 (UPS).
P. silvicola: Oregon, Tillamook Co., 3 (UPS).
Prometheomys schaposchnikovi: USSR, Georgian SSR, 1.
Synaptomys cooperi: Michigan, Washtenaw Co., 5.

The above-listed whole carcasses (all adults) were initially fixed in 10% buffered formalin or 70% alcohol and then stored in 70% buffered alcohol. Stomachs were removed for examination, bisected along the mid-frontal plane, and the contents washed out. Observations were made with a Baush and Lomb stereozoom microscope (10X–30X). I prepared the semidiagrammatic line drawings using a camera lucida. Anatomical terms employed in the description are defined as follows (see Fig. 1):

Incisura angularis – the pronounced angle formed by the dextral junction of the esophagus and stomach; corpus – that section of the stomach to the left of the incisura angularis; antrum – that section of the stomach to the right of the incisura angularis; fornix ventricularis – the portion of the corpus that extends cranially beyond the level of the gastroesophageal junction; bordering fold – a ridge or flap of cornified tissue that marks the juncture of glandular epithelium and cornified squamous epithelium, the two kinds of mucosal linings evident at the gross anatomical level.

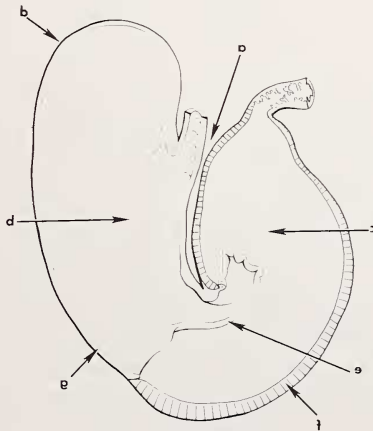


Fig. 1. The stomach of *Neofiber alleni* (UMMZ No. 110456) illustrating the following anatomical features: a = incisura angularis; b = corpus; c = antrum; d = fornix ventricularis; e = bordering fold; f = glandular epithelium; g = cornified squamous epithelium

Descriptions

Variation in three anatomical features accounts for most interspecific differences in gross configuration of the stomach. These features are: 1. the relative depth of the incisura angularis; 2. the development of finger-like projections on the free margin of the bordering fold; 3. the distribution of cornified squamous and glandular epithelia. In order to facilitate a concise description of the many forms examined, the nature of the variation encountered in each of these characters is described first and then summarized by species in the table.

The degree of compartmentation of the stomach is largely correlated with the depth of the incisura angularis. In certain forms, such as *Synaptomys cooperi* (Fig. 2 A), the incisura angularis is shallow and barely extends beyond the gastroesophageal opening. In this condition, the corpus and antrum are broadly continuous, and the stomach is basically a single compartment. In most specimens examined, I observed a deeper incisura angularis that extends at least one-half of the distance between the gastroesophageal junction and an opposite point on the greater curvature (Figs. 1 and 3). Such a pronounced incisura angularis forms a wall that partially divides the corpus from antrum and imparts a conspicuous bilocular configuration to the stomach. In the stomach of certain forms, for example, *Alticola roylei* (Fig. 2 B), the incisura angularis is intermediate to these two extremes.

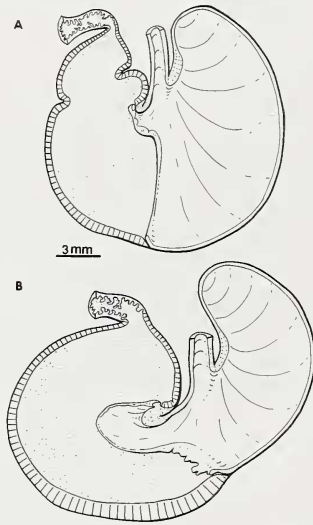


Fig. 2. A: The unilocular-hemiglandular stomach of *Synaptomys cooperi* (UMMZ No. 110434) and B: an intermediate stomach grade as exemplified by *Alticola roylei* (UMMZ No. 110405)

The bordering fold is situated at the junction of the cornified squamous and glandular epithelia and affords an easily discernable line of demarcation between them. In several species, for example, *Clethrionomys gapperi* (Fig. 5), this fold is a simple flap with its free edge even and smooth. In most specimens, however, the edge of the bordering fold is emarginate with short processes projecting over the glandular epithelium (Figs. 3 and 4). These processes are dentate or lobate in shape and usually are restricted to the left side of the glandular epithelium on the greater curvature. In examples of *Phenacomys*, the processes encompass much of the perimeter of the bordering fold that surrounds the diminutive glandular zone. The four species examined contrast in the extent of the bordering fold that exhibits these finger-like projections. The right side of the bordering fold has small, poorly-defined projections in specimens of *P. intermedius*; no such processes occur on the dorsal and ventral aspects of the fold in this species (Fig. 4 A). The entire rim of the bordering fold is dissected with elongate, filiform processes in the stomach of *P. albipes* (Fig. 4 c). The distribution of bordering fold pro-

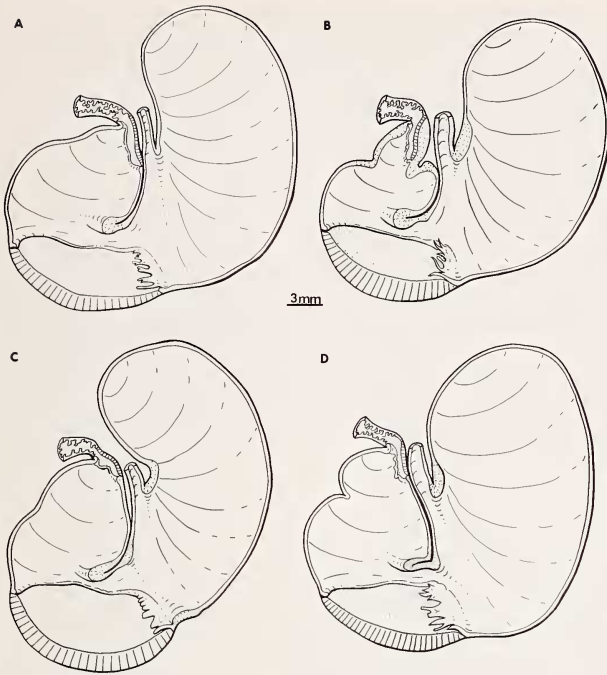


Fig. 3. Stomach morphology in four species of *Microtus*. A: *M. (Pedomys) ochrogaster* (UMMZ No. 110309); B: *M. (Chilotus) oregoni* (UMMZ No. 115618); C: *M. (Aulacomys) richardsoni* (UMMZ No. 110306); D: *M. (Pitimys) quaasiater* (UMMZ No. 113098)

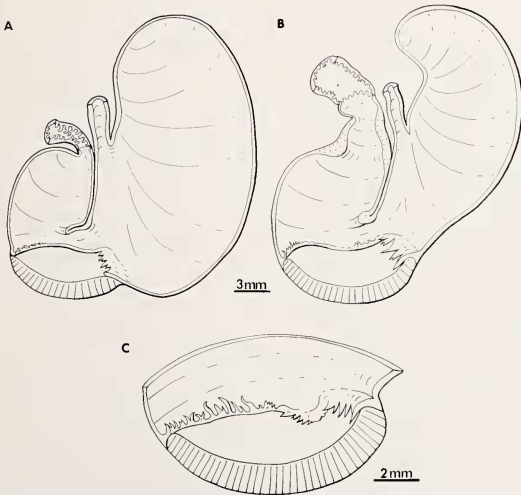


Fig. 4. Gastric structure in A: *Phenacomys intermedius* (UMMZ No. 110241) and B: *P. longicaudus* (UPS No. 5110); C: Enlargement of the glandular zone in *P. albipes* (UPS uncat.) showing the elongate processes of the bordering fold

cesses seen in examples of *P. longicaudus* and *P. silvicola* is intermediate to that observed in the above-mentioned species (Fig. 4B).

The distribution of glandular and cornified squamous epithelial linings varies greatly among the species examined. The largest extent of glandular epithelium was observed in the lemmings *Myopus schisticolor*, *Lemmus lemmus*, *L. obensis*, *L. sibiricus*, and *Synaptomys cooperi*. In these forms, glandular epithelium occupies the entire antral half of the stomach while cornified epithelium lines the corpus (Fig. 2A). Thus, the bordering fold approximately bisects the stomach on a line from the apex of the incisura angularis to an opposite point

on the greater curvature. Previously, I characterized this type of stomach as the hemiglandular condition (CARLETON 1973). The smallest area of gastric glandular epithelium occurs in *Dicrostonyx groenlandicus*, *D. hudsonius*, *Lagurus curtatus*, *Prometheomys schaposhnikovii* and species of *Phenacomys*. In examples of these, the glandular epithelium is restricted to a circular zone located on the greater curvature in the antral portion of the stomach (Fig. 4). The remainder of the stomach is covered with cornified squamous epithelium. I have termed this type of stomach the discoglandular condition (CARLETON 1973).

The apportionment of glandular epithelium in most species examined is intermediate to the hemiglandular and discoglandular plans. At least three intermediate grades can be discerned. In one, as exemplified by the stomach of *Alticola roylei* (Fig. 2 B), some cornified epithelium penetrates the antrum to the right of the incisura angularis but the majority of the antrum is covered with glandular epithelium. In another grade, as seen in *Clethrionomys gapperi* (Fig. 5 C), cornified epithelium lines approximately half of the antrum. A third grade is exhibited by *Ondatra zibethicus* and species of *Microtus*, which possess a small narrow patch of glandular epithelium on the lesser curvature near the pyloric orifice, in addition to the discoglandular zone on the greater curvature (Fig. 3).

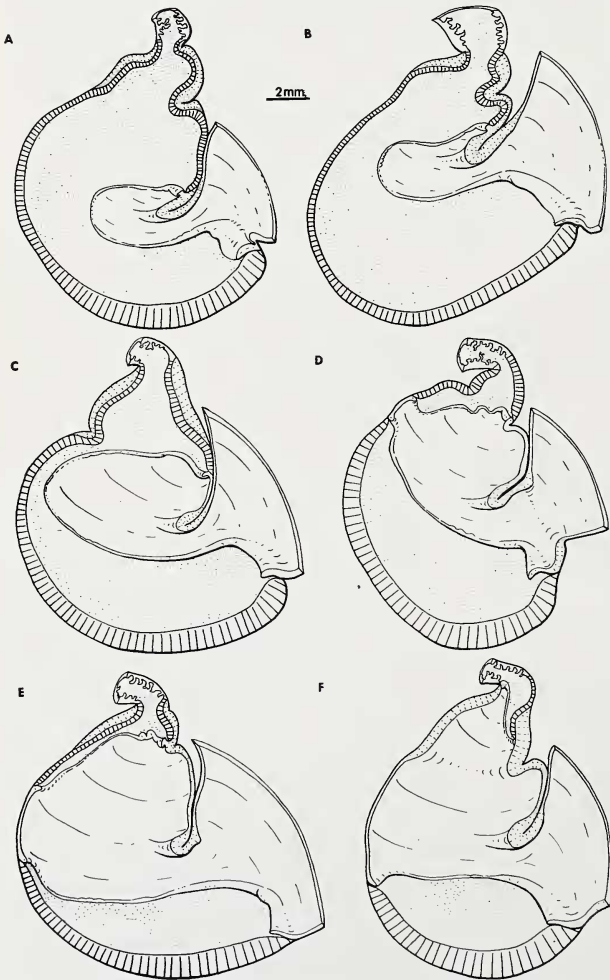


Fig. 5. Variation in extent of glandular epithelium in *Clethrionomys* (only the antral half of the stomach is portrayed). A: *C. glareolus* (UMMZ No. 97673); B: *C. gapperi saturatus* (UMMZ No. 75398); C: *C. g. gaspeanus* (UMMZ No. 108542); D: *C. g. gapperi* (UMMZ No. 55293); E: *C. g. gapperi* (UMMZ No. 87052); F: *C. g. gapperi* (UMMZ No. 87053)

Morphological state of the incisura angularis (IA), bordering fold (BF) and glandular zone (GZ) in stomachs of microtine rodents. Character state numbers are defined in the description

Species	Anatomical feature			Authority ¹⁻¹⁰
	IA	BF	GZ	
<i>Alticola roylei</i>	1	1	1	1,10
<i>Arvicola sapidus</i>	1	1	1	1
<i>Arvicola terrestris</i>	1	1	1	1,8,9,10
<i>Aschizomys lemminus</i>	?	?	1	10
<i>Clethrionomys gapperi</i>	2	0	1,2,3	1
<i>Clethrionomys glareolus</i>	2	0	1	1,6
<i>Clethrionomys occidentalis</i>	2	0	1	1
<i>Clethrionomys rufocanus</i>	2	0	1	1,6,10
<i>Clethrionomys rutilus</i>	2	0	3	1,5
<i>Dicrostonyx groenlandicus</i>	2	1	4	1,3
<i>Dicrostonyx budsonius</i>	2	1	4	1
<i>Dicrostonyx torquatus</i>	2	?	4	10
<i>Ellobius alacius</i>	1	0	2-3	1
<i>Ellobius fuscocapillus</i>	2	0	2	1
<i>Ellobius lutescens</i>	2	0	2	1,10
<i>Ellobius talpinus</i>	1	0	2-3	1,9
<i>Eothenomys melanogaster</i>	2	0	1	1
<i>Hyperacrius fertilis</i>	2	0	3	1
<i>Lagurus curtatus</i>	2	1	4	1,3
<i>Lagurus lagurus</i>	1	1	1	3,10
<i>Lagurus luteus</i>	1	1	1	10
<i>Lemmus amurensis</i>	?	0	4	10
<i>Lemmus chrysogaster</i>	2	1	4	10
<i>Lemmus lemmus</i>	0	0	0	1,9
<i>Lemmus obensis</i>	0	0	0	1
<i>Lemmus sibiricus</i>	0	0	0	1,3
<i>Microtus abbreviatus</i>	2	1	3	7
<i>Microtus afghanus</i>	2	1	3	1
<i>Microtus agrestis</i>	2	1	3	9
<i>Microtus arvalis</i>	2	1	3	1,8
<i>Microtus californicus</i>	2	1	3	1
<i>Microtus carruthersi</i>	2	1	4?	10
<i>Microtus chrotorrhinus</i>	2	1	3	1
<i>Microtus fortis</i>	2	1	3	1,10
<i>Microtus fulviventris</i>	2	1	3	1
<i>Microtus gregalis</i>	2	1	3	1
<i>Microtus guatemalensis</i>	2	1	3	1
<i>Microtus gud</i>	2	1	4?	10
<i>Microtus hyperboreus</i>	2	1	4?	10
<i>Microtus longicaudus</i>	2	1	3	1
<i>Microtus mexicanus</i>	2	1	3	1,4
<i>Microtus miurus</i>	2	1	3	1
<i>Microtus montanus</i>	2	1	3	1
<i>Microtus nivalis</i>	2	1	3	1
<i>Microtus ochrogaster</i>	2	1	3	1
<i>Microtus oeconomus</i>	2	1	3	1
<i>Microtus oregoni</i>	2	1	3	1
<i>Microtus pennsylvanicus</i>	2	1	3	1,5
<i>Microtus pinetorum</i>	2	1	3	1
<i>Microtus quasiater</i>	2	1	3	1
<i>Microtus richardsoni</i>	2	1	3	1
<i>Microtus savii</i>	2	1	3	1
<i>Microtus sikimensis</i>	2	1	3	1

Extensive variation in gastric morphology was observed among specimens of *Clethrionomys*, particularly the New World form *C. gapperi*. As reported by VORONTSOV (1962) and ORLOV (1968), the Old World species *C. glareolus* and *C. rufocanus* possess stomachs with a slight amount of cornified epithelium in the antrum (Fig. 5A). Additional samples of *C. glareolus* and *C. rufocanus* that I have examined agree with their descriptions and show no intra-specific variation. The one specimen of *C. occidentalis* available also fits this gastric pattern. On the other hand, the stomach of *C. rutilus* is discoglandular (ORLOV 1968). Examples of *C. gapperi* completely bridge the difference between the gastric pattern found in *C. glareolus*, *C. rufocanus*, and *C. occidentalis* and that seen in *C. rutilus* (Fig. 5B-F). This variation occurs within populations of *C. gapperi* as well as between them; for example the two specimens portrayed in Figs. 5E and 5F are from the same locality in Ontario.

In three instances, my findings disagree with previous reports on microtine gastric anatomy. These discrepancies involve the forms *Lemmus lemmus*, *L. obensis*, and *Myopus schisticolor* described by VORONTSOV (1962, 1967). He portrays a reduced area of glandular epithelium in these species while my observations reveal a hemiglandular pattern. TULLBERG (1899) studied *Myodes* (= *Lemmus*) *lemmus* and his representation of the stomach of that form concurs with my observations. Furthermore, DEARDEN (1969) has histologically examined the stomach of *L. trimucronatus* (= *sibiricus*) and demonstrated a basically hemiglandular distribution. I have not studied the other species of *Lemmus* that VORONTSOV (1962) figures as having diminutive areas of glandular epithelium. The stomach of my one example of *Myopus schisticolor* is clearly hemiglandular.

To recapitulate my observations on gross stomach morphology of microtine rodents, I have enumerated below the various states of morphological development observed in the incisura angularis, bordering fold, and area of cornified and glandular epithelia together with a code number for each state (Table 1). This tabulation includes species reported in the literature but not studied here. Where I could not determine precisely the anatomical configuration from the figures and/or descriptions of the authors, I have indicated a question mark

Table continued

Species	Anatomical feature			Authority ¹⁻¹⁰
	IA	BF	GZ	
<i>Microtus socialis</i>	2	1	3	1
<i>Microtus subterraneus</i>	2	1	3	1
<i>Microtus townsendii</i>	2	1	3	1
<i>Microtus ungurensis</i>	2	1	4?	10
<i>Microtus xanthognathus</i>	2	1	3	1
<i>Myopus schisticolor</i>	0	0	0	1
<i>Neofiber alleni</i>	2	0	1	1,9
<i>Ondatra zibethicus</i>	2	0	3	1,2
<i>Phenacomys albipes</i>	2	2	4	1
<i>Phenacomys intermedius</i>	2	1	4	1
<i>Phenacomys longicaudus</i>	2	2	4	1
<i>Phenacomys silvicola</i>	2	2	4	1
<i>Prometheomys schaposhnikovii</i>	2	0	4	1,10
<i>Synaptomys cooperi</i>	0	0	0	1
1 = species surveyed herein	6 = ORLOV 1968			
2 = BENSLEY 1902	7 = RAUSCH and RAUSCH 1968			
3 = DEARDEN 1969	8 = TOEPFER 1891			
4 = GENEST-VILLARD 1968	9 = TULLBERG 1899			
5 = GOLLEY 1966	10 = VORONTSOV 1962, 1967			

next to the coded state. The order of character states observes my interpretation of evolutionary polarities.

Incisura angularis: shallow (0); intermediate (1); deep (2).

Bordering fold: smooth (0); emarginate, processes concentrated on left rim of fold (1); emarginate, processes encompass entire rim of fold (2).

Glandular zone: hemiglandular (0); intermediate grade I (1); intermediate grade II (2); intermediate grade III (3); discoglandular (4).

Discussion

Variation in gastric morphology has been more thoroughly documented for the Microtinae than for any other major complex of Muroidea. No anatomical feature has been found peculiar to the stomachs of microtines that serves to distinguish them as a group separate from other muroids. An emarginated bordering fold is known to occur only in some microtines, but this elaboration is not ubiquitous. As a group, microtines exhibit the same evolutionary modifications in gastric anatomy evident in some other muroid assemblages. These include reduction in area of glandular mucosa (and concomitant augmentation of cornified epithelium) and increase in depth of the incisura angularis, imparting a bilocular condition (TOEPFER 1891; BENSLEY 1902; VORONTSOV 1957, 1962, 1967; GENEST-VILLARD 1968; CARLETON 1973). An increase in volume of the fornix ventricularis seemingly has accompanied change in the incisura angularis; however, this is difficult to demonstrate satisfactorily in view of the extreme distensibility of that section of the corpus, which varies according to the amount of food contained. Changes in the distribution of gastric mucosa, depth of the incisura angularis and size of the fornix ventricularis generally have evolved simultaneously, but this is not always true (CARLETON 1973).

Lemmings of the genera *Lemmus*, *Myopus* and *Synaptomys* possess basically unilocular-hemiglandular stomachs, the most generalized plan observed among microtines. Such a pattern occurs in all Gerbillinae examined, most Nesomyinae, most South American and Palearctic Cricetinae, and some neotomine-peromyscines (CARLETON 1973; DORST 1972; VORONTSOV 1967). The majority of Murinae studied to date also display this morphology (GENEST-VILLARD 1968; TULLBERG 1899; VORONTSOV 1962), but too few species of this vast group have been surveyed to allow generalization. The association of these three genera on the basis of similarity in gastric structure concurs with their previous alignment based on other data (HINTON 1926; HOOPER and HART 1962; KESNER 1977).

Examples of most microtines studied have stomachs with at least some diminution of the glandular zone and a more strongly pronounced incisura angularis (Table 1). Many, but not all, species with a reduced glandular complement also have an emarginate bordering fold, clearly a derived trait. No processes were observed on the bordering fold of forms having hemiglandular stomachs.

The bilocular-discoglandular stomach found in the collared lemming *Dicrostonyx* distinguishes it from other lemmings. Although traditionally placed in the same tribe as *Lemmus* and *Synaptomys* (Lemmi of MILLER 1896 or Lemmini of SIMPSON 1945), numerous authors have drawn attention to the distinctiveness of *Dicrostonyx* (HINTON 1926; HOOPER and HART 1962; KESNER 1977; KRETZOI 1955). Information derived from gastric morphology further emphasizes its fundamental separation from the other genera of lemmings.

The stomach observed in examples of *Lagurus curtatus* contrasts with that seen in *L. lagurus* and *L. luteus*. This divergence exceeds that recorded for any other genus of Microtinae, with the exception of *Clethrionomys* (see below). THOMAS (1912) diagnosed the subgenus *Lemmiscus* to contain the North American form *curtatus*, based on its longer tail and the occurrence of four prisms (instead of five as in Old World *Lagurus*) in the lower third molar. DAVIS (1939) proposed elevation of *Lemmiscus* to generic status, listing many characters

(among them development of a stapedia canal, complexity of the third molar, lack of cement, and presence of an antitragus) by which *Lemmiscus* differs as much from typical *Lagurus* as from *Microtus*. However, DEARDEN (1958, 1959) found no basis for generic segregation of *curtatus* from *Lagurus*, and this opinion has prevailed in the recent literature (JONES et al. 1975). The distinction in gastric anatomy again raises the question of the relationship of *curtatus* to Old World *Lagurus* and how best to express that relationship taxonomically.

Species of *Microtus* are remarkably uniform in stomach morphology. Species sampled include representatives of the subgenera *Aulacomys*, *Blanfordimys*, *Chilotus*, *Chionomys*, *Herpetomys*, *Pedomys*, *Phaiomys*, *Pitimys* and *Stenocranius*, many of which have been variously treated as separate genera. Examples of all, including the nominative subgenus *Microtus*, have basically discoglandular stomachs with emarginate bordering folds (although species differ in the shape of these fimbriations—Fig. 3). The astonishing point of resemblance, however, is the persistence of what appears to be a remnant of gastric glandular mucosa near the pyloric orifice in all specimens of *Microtus* examined.

The status of the North American water vole *richardsoni* deserves mention in view of its conformity in gastric structure to other *Microtus* and divergence from species of *Arvicola*. Although usually classified in the subgenus *Aulacomys* of *Microtus* (ELLERMAN 1941; HALL and KELSON 1959), MILLER (1896) placed the North American form together with Old World water voles in *Arvicola* (treated then as a subgenus of an expansively-defined genus *Microtus*). Furthermore, a link with Eurasian *Arvicola* has been suggested by studies of dentition (ZIMMERMAN 1955), the glans penis (HOOPER and HART 1962), dermal sebaceous glands (QUAY 1968), behavioral drum-marking (JANNETT and JANNETT 1974) and comparative myology (KESNER 1977), and recent faunal listings have acknowledged this body of evidence for allocation of *richardsoni* to *Arvicola* (JONES et al. 1975). The generic assignment of *richardsoni* obviously carries significant import because of its zoogeographic implications. The issue clearly merits reexamination based not only on the distinction in gastric anatomy but also on the cranial and dental similarities that led systematists to associate *richardsoni* with species of *Microtus*.

Clethrionomys has been cited as the genus that embraces species most closely approximating the primitive morphotype of Microtinae (HOOPER and HART 1962). In form of the stomach, however, that distinction rests with *Synaptomys*, *Myopus* and *Lemmus*. Nonetheless, *Clethrionomys* is unique in the amount of inter- and intraspecific variation encountered. One species in particular, North American *C. gapperi*, contains morphological grades that span the differences observed between other species in the genus (namely *rutilus* versus *glareolus*, *rufocanus* and *occidentalis*) or between other genera of microtines. I cannot detect any geographical trend in gastric morphology, but the material at hand is too scattered and limited in sample size to discern such.

The most elaborate bordering folds were observed in examples of *Phenacomys* (Fig. 4), in which much or all of the fold is conspicuously serrated. JOHNSON (1973) employed this character, among others, to argue for generic separation of *Arborimus* (*albipes*, *longicaudus* and *silvicola*) from *Phenacomys intermedius*. The bordering fold in the former three species is more complicated than that in *intermedius*, yet the difference is only one of degree. Both *longicaudus* and *silvicola* are intermediate to *albipes* and *intermedius* with regard to pronouncement of this feature, which by itself does not constitute convincing evidence for generic recognition of *Arborimus*.

Data from gastric morphology is more in accord with the multitribal division of the microtines proposed by HOOPER and HART (1962), rather than the traditional dual tribal system, that is, Lemmi and Microti (MILLER 1896; HINTON 1926; ELLERMAN 1941). Support for the former arrangement is reflected in the hiatus between *Dicrostonyx* and *Synaptomys-Myopus-Lemmus* and the distinctiveness of *Neofiber* and *Ondatra*. *Clethrionomys*, *Eothenomys*, *Aschizomys* and *Alticola* are closely similar. *Hyperacrius*, except for its lack of fimbria on the bordering fold, and *Phenacomys* more closely resemble *Lagurus curtatus* and spe-

cies of *Microtus*. Nonetheless, the possibility of widescale parallelism in gastric adaptations must be admitted, as underscored by the occurrence of many species with a reduced glandular zone, some having emarginated folds (*Dicrostonyx*, *Lagurus*, *Phenacomys* and *Microtus*), some not (*Ondatra*, *Hyperacrius* and *Prometheomys*).

Within the Muroidea, microtines are recognized as consummate herbivores. Their trends in gastric adaptations have been analogized to those of ruminant artiodactyls and the need to accommodate large quantities of food rich in cellulose (VORONTSOV 1962, 1967). Indeed, microtine species are customarily relegated to an herbivorous trophic role in ecological studies of small mammals and investigations of competition within a rodent community. In view of their entrenched reputations as herbivores, it at first disturbs one's intuition to discover that microtines tested in the lab consistently demonstrated a higher digestive efficiency on a diet of seeds as compared to vegetative parts of dicotyledons and monocotyledons (BATZLI and COLE 1979). Or to learn that seeds and/or insects may constitute a significant portion of a vole's diet on an annual basis (BATZLI and PITEKKA 1971; GEBZYNSKA 1976; ZEMANEK 1972). These studies caution that the actual nutritional regimen of a small rodent may be more varied and complex than the standard trophic categories (herbivore, granivore, insectivore etc.) allow us to convey. Moreover, such investigations suggest that a straight-forward correlation of gastric anatomy and typological classifications of feeding habits, as has been attempted previously (BENSLEY 1902; VORONTSOV 1967), is unlikely or, at least, premature given our limited comprehension of digestive processes in muroid rodents.

VORONTSOV's (1962, 1967) comparison to ruminant gastric adaptations holds an immediately intuitive logic for muroid rodents. With a shift in diet from foods high in protein-lipid to ones high in cellulose, natural selection has favored a reduction of the acidic glandular zone and compartmentalization of the stomach to foster the existence of cellulolytic gastric symbionts. Microtines might qualify as the best evidence among muroids in support of VORONTSOV's hypothesis, in view of their accepted herbivorous nature and the common occurrence of a chambered stomach with a reduced glandular zone within the group.

Upon closer inspection, however, VORONTSOV's analogy suffers from a number of observations, some of which I have enumerated earlier (1973):

1. The stomach in most muroid rodents is not divided to the degree observed in artiodactyls or other mammals with ruminant-like digestion (LANGER 1974, 1979; MOIR 1968). Whereas the gastric glands are wholly segregated apart from the fermentation chamber in an artiodactyl's stomach, the reduced glandular zone in muroid rodents straddles the partition that accounts for the bipartite condition of their stomachs.
2. The area proximal to the pylorus is covered with cornified squamous epithelium in muroids having a reduced glandular area; in artiodactyls, gastric mucosa is continuous to the pyloric orifice.
3. Pyloric glands are absent from the stomachs of many muroids, particularly those that possess a discoglandular condition, but such glands are found in the abomasum of a ruminants' stomach.
4. Fermentation sites for digestion of cellulose in other mammals have evolved in two regions of the alimentary tract: the forestomach or the caecum, but are not elaborated simultaneously (JANIS 1976; MOIR 1968). Therefore, it is enigmatic to explain the evolution of two major fermentation vats in Muroidea because many species possess a compartmented, discoglandular stomach as well as a highly convoluted caecum. This is especially true for microtines, many of which exhibit the most strikingly sacculated caeca and elaborations of the large intestine observed among species of Muroidea (VORONTSOV 1962, 1967).
5. Because metabolic requirements increase relatively more with decrease in body size, the costs associated with adoption of full-scale, ruminant-like digestion may be energetically prohibitive for animals as small as typical rats and mice (JANIS 1976; PARRA 1978). From this perspective, it is interesting that the muroid having the most complicated stomach, at

least for those species surveyed to date, is *Lophiomyis imbausi*, which is among the largest forms of Muroidea (VORONTSOV 1967).

6. Lastly, although food habits have been described adequately for only a few species of Muroidea, the known diets do not necessarily sustain that predicted on the basis of their gastric anatomy (see CARLETON 1973).

The above observations, taken as a whole, challenge the analogy to ruminant gastric adaptations as an explanation of stomach modifications seen in muroid rodents. Establishment of other hypotheses must await additional basic research concerning the process of digestion in these rodents. Some of the more profitable areas of inquiry include: determination of the nature of microbial symbionts occurring in the alimentary canal and comparison of the microbial contents of the stomach and caecum; comparative histological and histochemical studies of species having different gastric types; investigations of gastric motility, direction of food passage, and rate of passage of different foodstuffs; elucidation of gastric secretory phases and acidity maintained; and finally, exposition of species' food habits that employ large sample sizes drawn throughout major seasonal fluctuations. Some of these topics for investigation are discussed further below (and see CARLETON 1973).

The need for culturing and identifying gastric symbionts, on a level comparable to that undertaken for ruminant-like mammals, is crucial to substantiating VORONTSOV's hypothesis. This kind of information could also address the notion that enlargement of the foregut occurred so that herbivores could harbor a microflora capable of detoxifying secondary plant compounds before they pass to absorptive regions of the intestinal tract (FREELAND and JANZEN 1974). Despite the abundance of muroid species, the number of such studies is appallingly few. The information available indicates a much lower diversity and density of microorganisms in comparison to that recorded for ruminant stomachs (CAMAIN et al. 1960; KUNSTYR et al. 1976). Moreover, the biochemical properties of the microorganisms isolated include hydrolysis of starch, glucose and some proteins but not the fermentation of structural polysaccharides such as cellulose and lignin. Nevertheless, this data was gathered from species (*Cricetomys gambianus* and *Rattus norvegicus*) that have a single-chambered, hemiglandular stomach. The possibility that cellulolytic bacteria exist in species with a bilocular, discoglandular stomach should be pursued.

Knowledge of gastric histology in microtines surpasses that available for any other group of Muroidea. The following species have been examined: *Clethrionomys rutilus* (ORLOV 1968); *Dicrostonyx groenlandicus* (DEARDEN 1966, 1969); *Lagurus curtatus* and *L. lagurus* (DEARDEN 1966, 1969); *Lemmus sibiricus* (DEARDEN 1966, 1969); *Microtus pennsylvanicus* (DEARDEN 1966, 1969; GOLLEY 1960); and *Ondatra zibethicus* (BENSLEY 1902). The stomachs of *Lemmus* and *Lagurus lagurus*, species with a broad area of glandular epithelium (hemiglandular and intermediate grade I, respectively), contain fundic, cardiac and pyloric glands, the three types commonly found in mammals (BENSLEY 1902). On the other hand, *Clethrionomys rutilus*, *Dicrostonyx*, *Lagurus curtatus*, *Microtus* and *Ondatra*, all forms with a reduced area of glandular mucosa (either intermediate grade III or discoglandular), apparently lack pyloric glands. The functional significance of the loss of pyloric glands begs for an explanation. The identity and significance of the narrow strip of glandular mucosa near the pyloric orifice also warrant attention. DEARDEN (1969) and GARON and PIERARD (1972) have interpreted this strip as duodenal mucosa that has invaded the stomach, while BENSLEY (1902) and GOLLEY (1960) labelled it as pyloric glands. The former opinion, if correct, implies profound functional modifications of the usual digestive process. However, variation in gross morphology, especially as observed in specimens of *Clethrionomys*, suggests that the narrow zone is indeed a remnant of gastric glandular epithelium, an interpretation that can be resolved easily by further histological study.

The architectural rearrangements inherent in the shift from a unilocular to a bilocular condition imply changes in gastric motility and the passage of food. The muscular walls of the corpus are thin and seemingly cannot exert substantial mechanical forces upon a bolus of

food (GOLLEY 1960; KUNSTYR et al. 1976). On the other hand, the thin, elastic nature of these walls is eminently suited to accommodate large amounts of food at a single feeding. Presumably, the distensibility and resultant storage capacity in forms with a pronounced fornix ventricularis are further enhanced.

BLACK and SHARKEY (1970), citing OWEN (1868), mentioned the presence of a reticular groove in the stomach of *Lemmus* sp., apparently the only rodent known to possess one. The reticular groove is a channel formed by muscular folds near the gastroesophageal opening and is found in ruminant artiodactyls and some other mammals with foregut fermentation. BLACK and SHARKEY (1970) postulated that the groove occurs as an obligatory adaptation in such herbivores to shunt milk past the fermentation chambers into the abomasum of suckling young, where it is digested normally. The sulcus undoubtedly functions in this manner in young animals, yet it is equally well-developed in adults and serves as a bypass for foods not requiring fermentation (MOIR 1968). I have not observed a reticular groove as a permanent feature within any species of microtine, including *Lemmus*, or other muroid examined (CARLETON 1973). However, I have observed a sulcus running from the esophageal opening to the antrum in some, but never all, specimens of many species of Muroidea, suggesting that the reticular groove is a facultative adaptation in these animals. DEARDEN (1966) has demonstrated a complex interrelationship of smooth and striated muscle fibers at the gastroesophageal junction in some microtines and found that some longitudinal striated muscle of the esophagus even extends deeply into the incisura angularis. Thus, it is conceivable that these rodents can selectively direct swallowed food into the corpus or antrum. In this regard, I have frequently noted a striking difference in texture and appearance between foods contained in the corpus and antrum. Whether this textural contrast reflects different classes of food, for instance, insects versus seeds or green plant parts, or varying lengths of chemical action is not known.

Several lines of evidence suggest that the vast expanse of cornified epithelium in a muroid's stomach functions to sustain digestion of starch and/or glycogen rather than to provide a surface for cellulolytic microbes. The reduction of glandular epithelium could prolong the action of salivary amylase on glycogen and starch in ingested foods. In mammals with a wholly glandular stomach, salivary amylase, requiring a pH medium close to neutrality, is relatively quickly inactivated by the low pH maintained by hydrochloric acid from the fundic glands (DAVENPORT 1966). In *Rattus norvegicus*, a species with a hemiglandular stomach, a pH of five has been recorded in the cornified area of a recently-filled stomach compared to three in the glandular region (KUNSTYR et al. 1976). In addition, KUNSTYR et al. (1976) discovered that salivary amylase activity in the rat greatly exceeds that recorded for humans and concluded that the forestomach (= corpus) of the rat primarily allows the continual hydrolysis of dietary carbohydrates into simple sugars. By extension, one predicts that the disparity in pH between the corpus and antrum and resultant protraction of carbohydrate digestion would be greater in a stomach with a deep incisura angularis, diminutive glandular zone and spacious fornix ventricularis. A relationship to salivary amylase secretion is also intimated by differences in the salivary glands of some species of Muroidea and the apparent correspondence of those dissimilarities to gastric types (SIUDA and SZYMANSKA 1961; CARLETON 1973). Furthermore, the need to prolong the digestion of starch in seeds is consistent with the demonstrated slower rate of seed passage through the alimentary canal in comparison to green plant parts (KOSTELECKA-MYRCHA and MYRCHA 1964) and the higher digestibility of seeds (BATZLI and COLE 1979). What needs to be clarified is whether the retention time of seeds in the stomach is greater than that of green plants. In light of the retardation of seed passage, it may be worthwhile to determine the function of the processes on the bordering fold found in many microtines. Various baffles, folds and flanges have evolved in mammals with ruminant-like digestion, which impede the passage of digesta and thereby increase the time available for microbial action (LANGER 1974, 1979). Although the fimbria on the bordering fold usually lie prostrate upon the glandular mucosa, they have been noted to stand erect in cer-

tain individuals, offering some obstruction between the corpus and antrum (for example, see Fig. 3 B). The fact that muscularis mucosae penetrates these processes of the bordering fold (DEARDEN 1969) and that they are longest and most numerous at the constriction between the corpus and antrum offers circumstantial support for a role in physically retarding the passage of a food bolus.

Are microtines consummate herbivores? Their prismatic, ever-growing molars and capacious caeca obviously reflect the importance of selection for processing fibrous plant material. Nonetheless, once a seed is husked, their hypsodont dental batteries may be equally efficacious in masticating seeds as in grinding grasses and forbs. What emerges from this review is a picture of rodents able to efficiently assimilate a wide spectrum of foodstuffs, not ones narrowly specialized on certain classes of food. On the basis of current evidence, the sum of digestive adaptations in muroid rodents argues as much, if not more, for flexibility in feeding habits as for stenotrophy, a theme developed by earlier hypotheses (BENSLEY 1902; VORONTSOV 1962, 1967). LANDRY (1970) has stressed this point for the entire Order Rodentia but it bears reemphasizing especially for the Muroidea. The ability of muroid rodents to nutritionally accommodate a variety of food resources and seasonal fluctuations in availability of those resources may eventually prove a key to understanding the evolutionary success of the Muroidea relative to such groups as the Geomyoidea, Dipodoidea and Gliroidea.

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Zusammenfassung

Eine Untersuchung der Magenformen von Microtinae (Rodentia: Muroidea)

Die Magenform von 55 Microtinen-Arten (Rodentia, Muroidea) aus 16 Genera wurden untersucht. Die meisten Arten stellen—in Ergänzung zu VORONTSOV's Erhebung über Arten der alten Welt—nordamerikanische Arten dar. Die Befunde ergeben: Die Trennung von *Dicrostonyx* von *Synaptomys*, *Myopus* und *Lemmus*; einen Gegensatz zwischen *Lagurus* der neuen und alten Welt; die Ähnlichkeit der nordamerikanischen Schermaus mit anderen *Microtus*-Arten und ihre Abweichung von *Arvicola* der alten Welt; eine große Diversität zwischen Individuen von *Clethrionomys*. Insgesamt sprechen die magenanatomischen Daten eher für eine „Mehrstammes-Klassifikation“ als für eine „Zweistammes-Klassifikation“ der Microtinae. Die funktionelle Bedeutung der nachgewiesenen magenanatomischen Unterschiede wird diskutiert.

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Zur stammesgeschichtlichen Herkunft von *Hylochoerus meinertzhageni* Thomas (Suidae, Mammalia)

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Abstract

*On the origin of the giant forest hog *Hylochoerus meinertzhageni* Thomas (Suidae, Mammalia)*

An analysis of the skull, the dentition and the ethology of the African forest hog (*Hylochoerus meinertzhageni* Thomas) suggests, that this species is a secondary forest inhabitant. This assumption is confirmed by the phyletic origin. *Hylochoerus* is an offshoot of the *Mesochoerus* (= *Kolpochoerus*)-group of the African Plio-Pleistocene, as demonstrated by COOKE and WILKINSON (1978) and HARRIS and WHITE (1979). The *Mesochoerus* species occurred in a savannah-like biotop. Because *Mesochoerus limnetes* is something too specialised for an ancestor of *Hylochoerus*, an origin in the Late Pliocene is more probable than in the Lower Pleistocene.

The recurring changes of the vegetation in tropical Africa during the Pleistocene appears to be the reason of the secondary forest life of *Hylochoerus*. This secondary forest life is an explanation for the evolutionary level in the dental structure, the skull, the brain and in the ethological pattern. Therewith the day-activity is also explained.

Einleitung und Problemstellung

Das afrikanische Riesenwaldschwein (*Hylochoerus meinertzhageni* Thomas, 1904) wurde als Urwaldbewohner erst zu Beginn des 20. Jahrhunderts entdeckt. Die Merkmalskombination macht die generische Trennung von den übrigen Gattungen der Suidae notwendig. *Hylochoerus* steht morphologisch in manchen Merkmalen zwischen *Potamochoerus* bzw. *Sus* einerseits und *Phacochoerus* andererseits. Diese Merkmalskombination hat auch zu unterschiedlicher Beurteilung der taxonomischen Stellung und der stammesgeschichtlichen Herkunft von *Hylochoerus* geführt, indem diese Gattung einerseits mit der *Potamochoerus*-Gruppe in Verbindung gebracht, andererseits als primitiver Abkömmling des *Phacochoerus*-Stammes angesehen wurde (vgl. THENIUS 1970, 1979). Bereits THOMAS (1904; S. 195) schreibt, daß die nähere Untersuchung von Schädel und Gebiß „indicates that the animal is a link connecting the two groups (*Potamochoerus*-*Sus* und *Phacochoerus*), with an undeniable and perhaps ancestral relationship to *Phacochoerus*. It would, in fact, appear to be a survivor

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